Skeletochronological studies of cyclical growth of freshwater fishes in French Guiana. A review

by

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ABSTRACT. - This review draws together results obtained from studies of various fish species from French Guiana: *Arius couma*, *A. proops*, *A. parkeri* and *Hoplosternum littorale* (Siluriformes), *Leporinus friderici*, *Prosomyleus rhomboidalis* and *Tometes lebaili* (Characiformes). The skeletochronological approach provides data about their growth patterns. Some species display two growth cycles each year, whereas others have only one cycle. Whatever the annual growth scenario, the amount of food, abundant during the rainy seasons due to the flooding of the forest floor, probably regulates the growth rate. Skeletochronological techniques provide various biological data for fishes captured in the wild: growth performance, age at the first spawning, longevity and some biological characteristics of bone tissue.

RÉSUMÉ. - Études squelettochronologiques de la croissance cyclique des poissons dulçaquicoles de Guyane française. Une revue.

La revue regroupe les résultats de diverses études effectuées sur plusieurs espèces d'eau douce de Guyane française: *Arius couma*, *A. proops*, *A. parkeri* et *Hoplosternum littorale* (Siluriformes), *Leporinus friderici*, *Prosomyleus rhomboidalis* et *Tometes lebaili* (Characiformes). L'approche squelettochronologique a permis d'acquérir des données sur leur modèle de croissance. Certaines espèces présentent deux cycles complets de croissance par an, alors que d'autres n'en ont qu'un seul. Quel que soit le scénario de croissance, c'est la quantité de nourriture disponible, abondante durant la saison des pluies dans les sous-bois inondés, qui semble réguler les performances de croissance. Quoi qu'il en soit, les techniques squelettochronologiques procurent des données biologiques variées sur les espèces capturées dans le milieu naturel : vitesse de croissance, âge d'acquisition de la première maturité génitale, longévité et quelques caractéristiques biologiques des tissus osseux.

Key words. - Siluriformes - Characiformes - French Guiana - Skeletochronology - Cyclical growth.

In temperate countries bony fish have a circannual growth cycle that is characterized by typical growth marks ("zones", "*annuli*"; see Baglinière *et al*., 1992; Panfili *et al*., 2002) on various bones (e.g., operculars, vertebrae, fin rays etc.), scales and otoliths (Casselman, 1987; Meunier, 1988; Castanet *et al*., 1992, 1993; Panfili *et al*., 2002; Green *et al*., 2009). These growth cycles are synchronized with the seasons and, more specifically, with annual variations of temperature and photoperiodicity (Castanet *et al*., 1977; Bourlière, 1980; Panfili *et al*., 2002). In tropical regions the annual variations of these two physical parameters do not occur or their amplitude is small. So one could speculate that under these conditions neither growth cycles nor growth marks would be observed, but this is not the case. In fact, various exogenous influences may regulate increment formation in the otoliths of tropical fish (Panfili *et al*., 2009). For example, a weak but regular variation of temperature amplitude, of around 4°C, was found sufficient to regulate body growth in *Lethrinus nebulosus*, a lethrinid of the New Caledonian lagoon, and to result in growth mark deposition in otoliths and also in finrays (Meunier *et al*., 1979). Another widespread annual climatic parameter in tropical regions, the alternance of wet and dry seasons, is responsible for a marked seasonality and can result in growth marks in the mineralized organs, as for example in teleost fish living in rainy tropical forests (Lowe-MacConnell, 1964, 1987; Blake and Blake, 1978; Robben and Thys van den Audenaerde, 1984; Loubens and Panfili, 1992; Meunier *et al*., 1997).

Several freshwater and euryhaline fishes of French Guiana, have an important halieutic interest (Mérona *et al*., 2001) and some other species show potential for aquaculture (Boujard *et al*., 1988). Among these, the "Atipa" (*Hoplosternum littorale*) has already been the subject of rearing experiments (Luquet *et al*., 1989; Hostache *et al*., 1990; Ramnarine, 1994a, 1994b). During the three last decades, ecological and biological studies performed in the field have aimed to improve the knowledge of these species in order to plan for rational management of the natural stocks; we can cite various Ariidae (Lecomte *et al*., 1985, 1986, 1989), Callichthyidae (Meunier *et al*., 2002) and Characiformes (Boujard *et al*., 1991; Lecomte *et al*., 1993; Lord *et al*., 2007). In French Guiana, with respect to possible fish farming, most data were obtained for the Atipa based on studies performed by the INRA team during the nineties (Hostache *et al*., 1990, 1992, 1993, 1995; Pascal *et al*., 1994, 1995; but see also the papers of some other South American scientists:

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Cybium 2012, 36(1): 55-62.

Ramnarine, 1994a, 1994b; Mol, 1996).

Both the management of the natural fish populations and fish farming require a good knowledge of the growth characteristics and the constraints on the animal in its environment. For that purpose ageing animals, evaluating the time between birth and any moment of life (time between birth and death corresponds to longevity), is a necessity (Casselman, 1987; Panfili *et al*., 2002; Fowler, 2009). To assess the age of wild fishes we can use size frequencies methodology (Petersen, 1892), but this method requires abundant material and its biological information is limited (Castanet *et al*., 1993). However, measuring individual age using sclerochronological techniques can be done with any sample size (Panfili *et al*., 2002); moreover, these techniques generally provide more biological data for each individual (Castanet *et al*., 1993; Meunier, 2002; Fowler, 2009).

Ageing of Guianese freshwater fishes

Individual ageing of tropical teleost fish specimens can be done using mineralized tissue because such tissues behave as natural recorders of various physico-biological data (Panfili, 1992; Castanet *et al*., 1992, 1993; Campana, 2001; Fowler, 2009). However, the choice of organs for sclerochronological investigations is of major importance for any growth studies in natural environments. The mineralized elements commonly used for ageing teleost fish are the otoliths (otolithometry), the scales (scalimetry) and sometimes bones (skeletochronology) such as the opercular, vertebrae, and spiny rays (e.g., Meunier, 1988; Castanet *et al*., 1992, 1993; Panfili *et al*., 2002; Green *et al*., 2009). In scaleless species of Siluriform, where the otoliths are not suitable for ageing, the histology of bony tissues was analysed in order to obtain histological data related to growth and longevity (Marzolf, 1955; Van Der Waal and Schoonbee, 1975; Moltschaniwskyj and Cappo, 2009). The best bones are the spiny rays but sometimes reabsorbtion processes can lead to age under-estimation (Castanet *et al*., 1992, 1993; Panfili *et al*., 2002).

For Guianese fish species the choice is often restricted to a single organ. In Characoids the small otoliths do not provide the pertinent information and scales are currently used for ageing (Cordiviola, 1966; Werder, 1984; Loubens and Panfili, 1992). However, in some characiforms (*Leporinus friderici*, *Prosomyleus rhomboidalis* and *Tometes lebailli*), a large number of scales are regenerated and are thus inappropriate for accurate age estimation. Another method can be the use of some adapted bones. For example, in the anostomid *Leporinus friderici*, the dorsal and anal fin-rays and the opercular bone (Fig. 1) show well-defined growth marks that were used for ageing (Lecomte *et al*., 1986; Boujard *et al*., 1991). However, studying fin rays is time consuming when compared to a direct observation of the operculars (Fig. 1). In the serrasalmid "Coumarou" (*Prosomyleus rhomboidalis*) the scales are small and frequently regenerated, and the fin-rays provide inconsistent information, in contrast to the opercular bone, which shows regular growth marks (Lecomte *et al*., 1993). In another serrasalmid, the Watau Yaike (*Tometes lebaili*), the vertebrae show distinct concentric growth marks (wide zones corresponding to active growth and thin zones of slow growth zones or *annuli*) that allow assessment of the age of each individual (Fig. 2); in older fishes, however, the

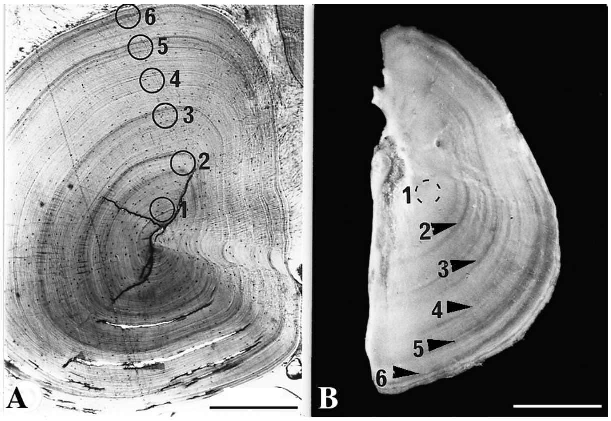

Figure 1. - *Leporinus friderici*. Comparison of the growth marks on a dorsal fin ray (**A**) and an opercular (**B**). Scales bars: A = 300 µm; B = 1 cm.

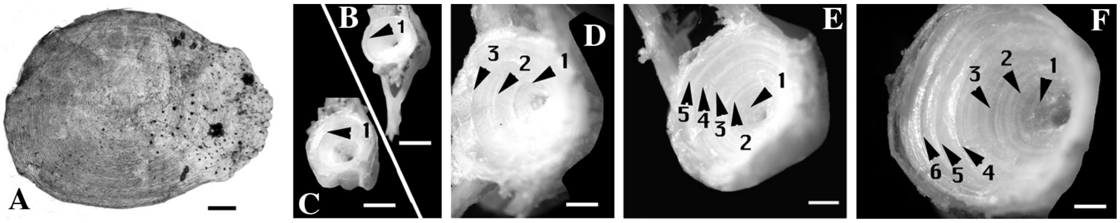

Figure 2. - *Tometes lebaili*. **A**: Scale of specimen MNHN 2002-0825 (4^+; observed in transmitted light): the *annuli* are hardly visible; **B-F**: Vertebrae observed in reflected light on a dark background. Arrow heads point to the *annuli*; **B**: Specimen MNHN 2003-34, SL: 82 mm; a single *annulus* is present and located at the margin of the vertebra; **C**: Specimen MNHN 2003-31, SL: 105 mm; the only *annulus* is far away from the vertebra margin; bone growth has clearly resumed; **D**: Specimen MNHN 2002-929, SL: 242 mm. Three *annuli* are present, the last one being far away from the vertebra margin; **E**: Specimen MNHN 2002-818, SL: 288 mm. Five *annuli* are present, the last one is relatively close to the vertebra margin; **F**: Specimen 2001-1222, SL: 416 m. Six *annuli* are present, the last one being far away from the vertebra margin. (Scale bars = 1 mm). (From Lord *et al*., 2007).

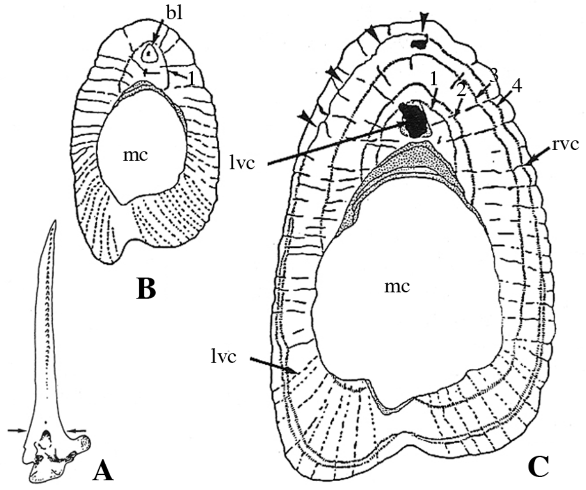

Figure 3. - *Arius proops*. **A**: Posterior view of the pectoral spiny ray showing the level of sectioning for ageing (arrows); **B**: Cross section of a spiny ray in a young individual. The formation of a second *annulus* is imminent; **C**: Drawing of a cross section of a spiny ray in an older fish showing four *annuli* (1-4). The medullar cavity (mc) has developed at the expense of primary periostic bone; Dotted areas delineate secondary bone. (bl = birth line; lvc = longitudinal vascular canal; rvc = radial vascular cavity). (From Lecomte *et al*., 1989).

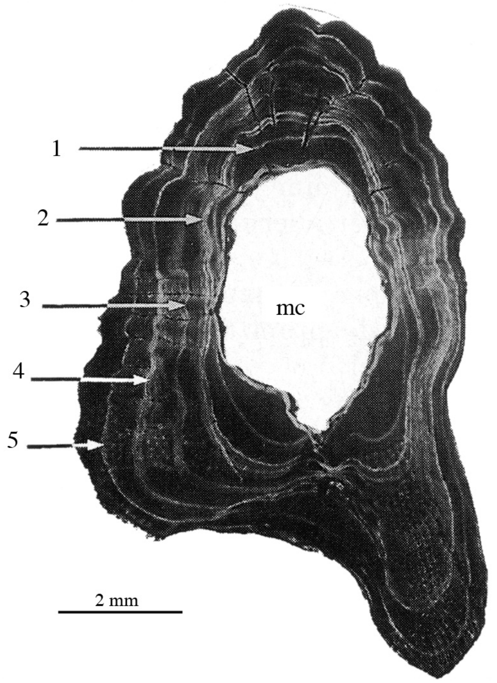

Figure 4. - *Arius parkeri*. Male, 79 cm SL. Transverse section of pectoral spiny ray, observed in transmitted light, showing 5 *annuli* (1-5); (mc = medullar cavity) (Scale bar = 2 mm). (From Meunier *et al*., 1997).

operculars are subject to important reabsorbtion which leads to underestimates of age (Lord *et al*., 2007). In scaleless Ariidae, the most useful biological tool is the spiny ray (Fig. 3) (Meunier *et al*., 1997). The same character was found efficient for the Callichthyidae (Meunier *et al*., 2002), even if the dermal plates of the skin also show growth marks (Sire *et al*., 1993).

Therefore, thanks to the skeletal support, we can study the growth of fish in their natural environment, estimate their age and their longevity as well as their age at the first gonadic maturation (for example: Lord *et al*., 2007).

Ageing methodology and techniques

The techniques used for otolithometry and scalimetry are well known and it is not necessary to describe them here. In particular, they were clearly detailed in specialized handbooks (see Panfili *et al*., 2002; Fowler, 2009; Panfili *et al*., 2009). Skeletochronology is, however, less common as it is generally only performed when the two above techniques are unsuitable ageing purposes. It is, therefore, necessary to point to some difficulties that could appear when applying this technique and as well as highlighting the advantages (Castanet *et al*., 1992, 1993).

The opercular bones (like any flat bones in fish) are relatively thin and easy to dry. They were studied *in toto* using reflected light on a black background, sometimes immerged in glycerinate alcohol or essential oils (rosemary oil or anise oil, for example) to improve the contrast of the growth marks. In ariids, the spiny rays were dried, then cut mechanically and studied with reflected light in a clearing glycerinated alcohol (Fig. 4). In the callichthid Atipa one pectoral spiny ray was dried and cut, and the other ray was decalcified with nitric acid, cut using a freezing microtome and the section stained with Erlich hematoxylin (see Meunier *et al*., 2002) according to the methodology currently used for the sections of tetrapod long bones (Klejnenberg and Smirina, 1969). This technique reveals the lines of arrested growth (= LAGs or rest lines) (Fig. 5) that belong to the “cementing lines” family (Castanet, 1981). These chromophilic LAGs are generally hypermineralized, they appear either inside *annuli* or alone and they alternate directly with the zones (Castanet *et al*., 1992, 1993). When hypermineralized, the LAGs can be revealed on microradiographs of undemineralized bone sections and they are an interesting skeletochronological tool (Meunier *et al*., 2002).

Whichever technique is used, bone sections allow histophysiological interpretations deduced from the structural characteristics of bony tissues (Ricqlès *et al*., 1991). Indeed, the histological features of fish bone depend on various constraints (Meunier *et al*., 2008): intensity of metabolism, growth speed, physiological state of the animal, age, etc. (Castanet *et al*., 1993). These data are of particular interest when fish biology is unknown, or at best poorly known, as is frequently the case for the teleosts living in the rivers of French Guiana.

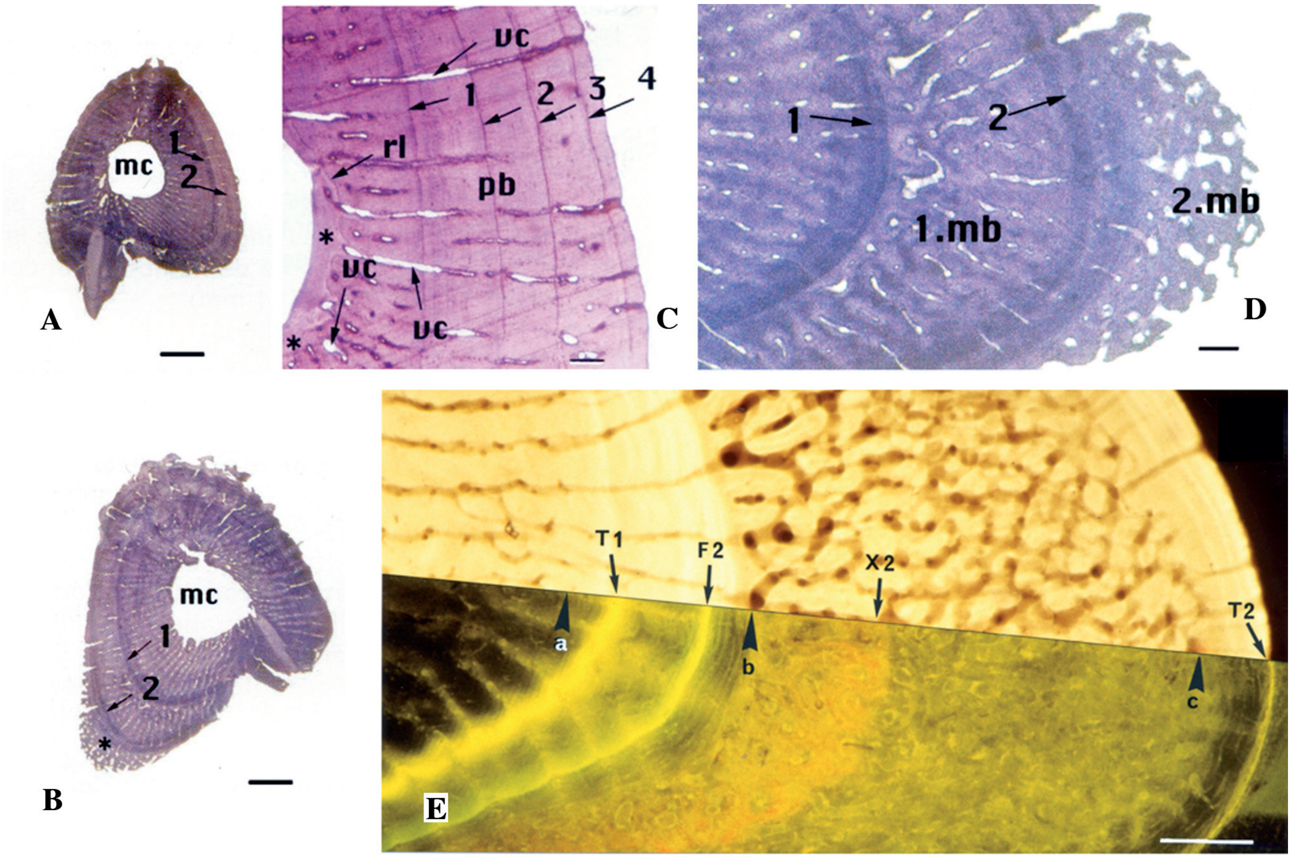

Figure 5. - *Hoplosternum littorale*. **A-B**: Cross sections of pectoral spiny rays in a female and a male, respectively, showing two *annuli*: age class 2^+ (hematoxylin); **C**: Female. Detail of a section showing four lines of arrested growth (1-4): age class 4^+; the stars underline secondary bone; **D**: Male. Detail of a section showing two patches of maturing bone (1.mb et 2.mb) characterized by an abundant vascularization; two *annuli* are visible (1-2): age class 2^+; **E**: Section of a spine in an experimental male fish (see Boujard and Meunier, 1991) regularly injected every two months with vital dyes: tetracycline (T1 and T2), fluorescein (F2) xylenol orange (X2); note the difference of bone deposit speed (= osteogenesis) between a-b (poorly vascularized bone: 1-2 μm per day) and b-c (hypervascularized bone: till 20 μm per day) (From Meunier *et al*., 2002). Scale bars: A, B = 1 mm; C, D, = 250 μm; E = 200 μm.

Table I. - Some biological data obtained with skeletochronological methods for several French Guianese fish species (Characiformes and Siluriformes) observed in the field: maximal standard length (SL; cm); longevity (Lg); age at first sexual maturity (A-SL 1st Mat); observed annual growth. (1: Lecomte *et al*., 1986; 2: Lecomte *et al*., 1993; 3: Lord *et al*., 2007; 4: Meunier *et al*., 2002; 5: Lecomte *et al*., 1989; 6: Lecomte *et al*., 1985; 7: Meunier *et al*., 1997).

Species	SL	Lg	A-SL 1st Mat	Annual growth						
				1	2	3	4	5	6	7
Leporinus friderici (1) Anostomidae			1-2	36	4.5	2	18	8	7	2
Prosomyleus rhomboidalis (2) Serrasalmidae	38	5	1*	13	7	9	5	2		
Tometes lebaili (3) Serrasalmidae	51.2	> 8	3-4	12.5	8.8	3.0	3.5	5.8	4.9	3.5
Hoplosternum littorale (4) Callichthyidae	21.8	3-4	1	19.4	2.4					
Arius proops (5) Ariidae	69	3.5	1.5	35	23	8				
Arius couma (6, 7) Ariidae	80	4,5		28	18	16	6			
Arius parkeri (7) Ariidae	119	4	2	46	22	26				

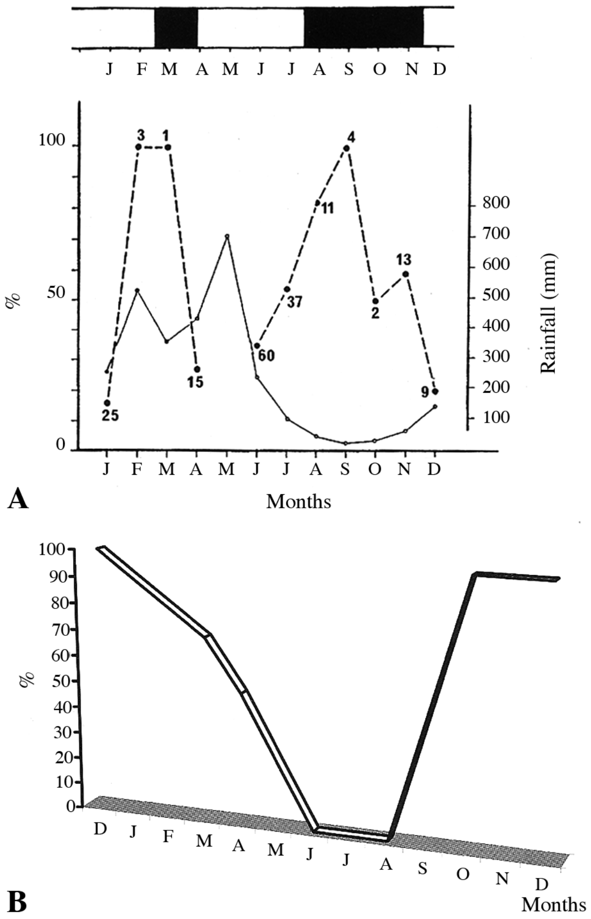

Figure 6. - **A**: *Arius proops* annual variations (1982) of the monthly rainfall (full line) and the percentage of specimens with *annuli* at the margin of the pectoral ray (dotted line). The number at each point gives the number of specimens studied; on the top alternance and duration of the wet (black) and dry (white) seasons along the year. (From Lecomte *et al*., 1986); **B**: *Hoplosternum littorale*. Percentage of males showing a regular deposit of genital maturing bone at the margin of the pectoral spiny ray along the year (from Meunier *et al*., 2002).

External factors, growth cycle synchronisation and their validation

It is generally recognized that fish growth displays two phases per year: in temperate areas a fast growth phase occurs from spring to early autumn and a slow growth phase from autumn to the end of winter, while in wet tropical lands this seasonal alternance is represented by the rainy and dry seasons. In this case the availability and/or the amount of food regulate growth performance. During the rainy season the rivers overflow the adjacent forest floor, providing many food items (Junk, 1975 *in* Werder, 1984; Lowe-McConnell, 1979, 1987) for phytophagous or invertebrate-feeding animals. Active growth related to abundant food results in the rapid deposition of bone matrix revealed by growth zones. During the dry season, the river returns to its bed and food availability decreases, often drastically. Then fish growth slows down and eventually stops, which is reflected in a slow deposition of bone matrix appearing as slow growth zones or *annuli*. These *annuli* can be reinforced by a LAG in bones or can be reduced to only a LAG (Meunier *et al*., 1997).

In French Guiana, however, the scenario can be different as some teleost fish species seem to show two fast growth periods alternating with two slow growth periods during a year (Lecomte *et al*.,1985, 1986; Meunier *et al*., 1997); interestingly these bimodal cycles are synchronous with the two rainy and two dry seasons, respectively (Fig. 6A) (see Boyé *et al*., 1979). For example, Coumarou populations studied in the lower part of the Sinnamary and Approuague river basins exhibit two growth phases during a year (Lecomte *et al*., 1993). Similar findings were obtained with ariids (*Arius proops*, *A. couma* and *A. parkeri*) and several characiforms (*Leporinus friderici*, *Myleus ternetzi*) (Meunier *et al*., 1997). Each dry season mimics a "physiological winter" (Lowe-McConnell, 1964). In contrast with the above-cited species, the Atipa and the Watau Yaïke show only one growth cycle per year (Fig. 5B). The Atipa lives in the costal marshes, such as the "Marais of Kaw", whereas the Watau Yaïke lives in the upper part of the Maroni river.

Growth biology of Guianese freshwater fishes

Skeletochronological studies lead to the hypothesis of an annual growth scenario, which could be the starting point of numerous biological interpretations for the species studied. However, in theory these biological data remain speculations as long as experimental studies have not validated this growth scenario in the field (Beamish and McFarlane, 1983; Casselman, 1987; Panfili *et al*., 2002). An appropriate experimental validation would be the use of vital labelling (Campana, 2001; Panfili *et al*., 2002), but this method is not realistic in tropical rivers such as those in French Guiana because of the great scattering of experimental fish. This lack of experimental validation is unimportant when carrying out regular (monthly) fish sampling (Fig. 6A, 6B), since this method then provides an indirect validation of the growth scenario (Lecomte *et al*., 1993; Meunier *et al*., 1997; Lord *et al*., 2007). Overall, the skeletochronological studies of Guianese fish have delivered much interesting biological information.

The growth performances of the teleost species studied to date are grouped in table I. Whatever the maximal length in the adult, growth is rapid from the first year of life but longevity is relatively short. In both males and females the growth rate of bone decreases with age. In adults, this slowdown is more marked after a particular *annulus* that corresponds to the attainment of the sexual maturity and indicates that the fish have spawned for the first time (Castanet *et al*., 1977; Meunier *et al*., 1979). In the fish studied in French Guiana, sexual maturity is reached early in life, as expected for species with short longevity.

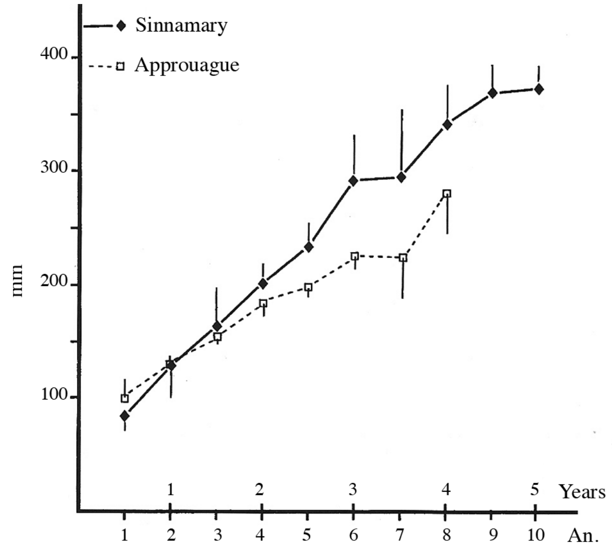

Figure 7. - *Prosomyleus rhomboidalis*. Growth curve of the Sinnamary River population (1982-1983), and Approuague River population (1986-1987). (From Lecomte *et al*., 1993).

The skeletochronological analysis of pectoral spiny rays of *Arius proops* revealed a slow growth period during March-April (the "little summer of March"; Boyé *et al.*, 1979) (Lecomte *et al.*, 1986). In French Guianese estuaries the longevity of this species is short: three and a half years for the females and three years for the males. The growth rate is relatively high during the first half of life (Lecomte *et al.*, 1989). Similar results were obtained for the largest species, *A. parkeri*, and for the more or less strictly freshwater ariid *A. couma* (Meunier *et al.*, 1997).

In the Atipa, the resting period corresponding to the slow growth bone-LAG deposit occurs from May to August-September (Fig. 6B). Its longevity in the field is about 3-4 years and it shows a fast growth phase during its first year (Fig. 5A-5C). First spawning of *Hoplosternum littorale* occurs at the age of 1^+ year (Meunier *et al.*, 2002); this result was experimentally confirmed using multiple vital labelling of reared specimens in outdoor ponds (Boujard and Meunier, 1991; Sire *et al.*, 1993). The males show a very specific characteristic of their pectotal spiny rays: an important deposit of spongy bone (= "genital maturing bone") appears during each great dry season; the females do not display such a feature (Fig. 5C-5E). This vascularized bone reveals a high speed of osteogenesis of 30-50 microns per day and is synchronized with sexual maturation in males (Boujard and Meunier, 1991). The link between these processes remains unknown, though endocrinal factors are probably involved. Such a secondary sexual character is proper to this species and indicates specific bone biology in males. It also allows an easier ageing of males (the number of vascularized bone deposits directly reveals fish age), in contrast to the females, in which ageing is more difficult (Meunier *et al.*, 2002).

The Coumarou, *Prosomyleus rhomboidalis*, displays an interesting growth potential in French Guianese rivers, although it is less important than in several other amazonian serrasalmids (Meunier *et al.*, 1997). Moreover the growth rate of *P. rhomboidalis* varies according to the rivers (Fig. 7) (Lecomte *et al.*, 1993). Its longevity is shorter than in the Watau Yaike (see below), but the first spawning of the Coumarou takes place earlier at 1^+ year.

In the Watau Yaike *Tometes lebaili*, the maximum age estimated using vertebrae growth marks (Fig. 2) is 8-9 years, with a maximal standard length is 512 mm. However, in the upper Maroni basin the lifespan of the Watau Yaike is probably underestimated because specimens measuring at least 600 mm SL were observed in another context but not studied (Lord *et al.*, 2007). The age at the first sexual maturity was estimated to be 3-4 years (Fig. 2F). This result is of importance as it implies that local Wayana people respect an interval of at least six years between two successive traditional fishing episodes[1] to allow adult fish to reproduce two to three times during their lifespan. Such a time limit seems to be sufficient to maintain a sustainable Watau Yaike stock.

Conclusion

Given that more than 480 fish species live in the French Guianese hydrosystems, (Planquette *et al.*, 1996; Keith *et al.*, 2000; Le Bail *et al.*, 2000), 80% of which are characiforms and siluriforms, the biological studies of the few species reviewed illustrate our lack of knowledge. The characteristics of these hydrosystems, with huge stretches of water of difficult access, do not make scientific field studies easy. Yet, some of these hydrosystems probably have an important biogeographical function (Meunier *et al.*, 1998, 2011; Jégu and Keith, 1998, 1999). Scientific efforts must be developed in order to improve the qualitative and quantitative data available, with the goal to set up conservation management both of the richness of French Guianese hydrosystems and of the stocks of significant species. In this regard, ageing techniques, and particularly skeletochronology, are of importance as they provide biological information on each fish species in the field.

Acknowledgements. - I thank very much John Hollier, Muséum d'histoire naturelle de la ville de Genève, and the anonymous referees who revised the English language and style.

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[1] Information about this traditional fishing by the Wayana people in the Upper Maroni basin are available in Meunier, 2004.

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